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AUSTRAL HEPATICAE XVIII. STUDIES TOWARD A REVISION OF *TELARANEA* SUBG. *NEOLEPIDOZIA* (LEPIDOZIACEAE)

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Telaranea here is broadly interpreted to include as subgenera *Telaranea s. str.*, *Acrolepidozia* (Schust.) Schust., *Neolepidozia* (Fulf. & Tayl.) Schust., and *Tricholepidozia* Schust. (cf. Schuster, 1963, 1969, 1972). Of these subgenera, *Neolepidozia* is the largest. Basically, this group includes taxa with incubous leaves inserted virtually to the dorsal stem midline, only a fraction of the two cell rows that lie contiguous to the dorsal stem midline remaining "leaf-free" (fig. 3: 1). These leaves, furthermore, possess a distinct disk, commonly 3–4 or even 7–9 cells high (figs. 1: 5–7; 3: 1,5), and typically, uniseriate lobes arising from a base often formed by two cells situated side by side (figs. 1: 5–7; 3: 1, 4–5). The leaves are quadrifid in the bulk of taxa, but exceptional taxa have trifid or even sexfid leaves. All taxa basically are delicate plants, with thin-walled leaf cells (figs. 1: 9; 3: 1) and a stem with a large-celled cortex formed of leptodermous cells (figs. 1: 4; 2: 3).

Subgenus *Neolepidozia* basically is circumsubantarctic in range, with most taxa in cool sectors of Australasia (ca. 17 species) and South America (four species). There has been limited dispersal northward, with one species, *T. (Neolepidozia) wallichiana* (Gott.) Schust., extending northward to Japan (Schuster, 1980) and a second, *T. (Neolepidozia) rectangularis* Schust., found as far north as the Venezuelan Andes (Schuster, 1978). As with other cool-adapted Gondwanalandic taxa, *Neolepidozia* is poorly represented in Africa, with at least one species, *T. (Neolepidozia) trifida* (Steph.) Schust. (Schuster, 1966, p. 105), occurring north to central Africa. A limited number of taxa occur in tropical parts of Australasia, with at least five species in New Guinea (Grolle, 1966). As interpreted here, subg. *Neolepidozia* is defined to include subg. *Chaetozia* Grolle (Grolle, 1966, p. 280) for reasons cited in Schuster (1972). So defined, it includes a minimum of 29 species, although a residuum of species, described chiefly by Stephani under *"Lepidozia,"* remain which need transfer to *Neolepidozia.*

Subgenus *Neolepidozia* is the most generalized within *Telaranea s. lat.*, the other three subgenera all showing striking specializations. As the most generalized group, it also is the only one within *Telaranea s. lat.* that shows a clear connection to other groups within Lepidoziaceae subfamily Lepidozioideae, especially to *Lepidozia.* In our opinion, however, *Telaranea s. lat.* is an adequately defined genus, differing from *Lepidozia* chiefly in the: (1) symmetric leaves, typically formed of relatively large, pellucid, and leptodermous cells; (2) marked tendencies for variations in leaf-lobe number, ranging from 2 to as high as 12–13; (3) consistent lack of any tendency toward production of teeth of leaf and/or lobe margins; (4) general development of a conspicuous hyaloderm of the stem; and (5) areolate spores in all examined taxa.

The two species treated on the following pages show all of these traits (except the last; they are not known from sporophyte-bearing material), and show the specific features cited in the first paragraph, which delimit *Neolepidozia.* One of the two species, *T. grossiseta*, is of particular interest in that it shows two phylogenetically sig-

nificant features: (1) It retains the ability to develop ventral-terminal, *Acromastigum*-type branching, which is of rare occurrence in the subfamily (Lepidozioideae) to which it belongs. Such branching has been seen in the allied genus *Lepidozia* only in subg. *Dendrolepidozia* Schust. (Schuster, 1972). In this, and in the high disk and relatively vigorous size, *T. grossiseta* is relatively primitive within *Telaranea s. lat.* (2) The form of the leaf, with a high and subsymmetric disk, and with setaceous leaf lobes, suggests subg. *Tricholepidozia*, in which, however, well-developed leaves possess 8–13 lobes rather than 4, and in which the hyaloderm is much less distinct. Thus, *T. grossiseta* may lie near the base of the genus *Telaranea* and surely is the least specialized species known at present in a relatively highly derivative genus. It is of particular interest in that the basic criteria exhibited by this species (conspicuous hyaloderm, subsymmetric leaves, leptodermous cells which are strikingly elongated in the lobes, setaceous leaf lobes) are quite typical of *Telaranea*. Hence, even at the level of this species, the distinctions between *Telaranea* and *Lepidozia* are already well marked. This fact is relevant in demonstrating that, even though some students still are reluctant to accord *Telaranea s. lat.* the rank of a genus distinct from *Lepidozia*, the generic distinctions are obvious at this level.

The second species, *T. tuberifera*, is of special interest in that, even though it is a "typical" *Neolepidozia* in the four criteria just cited for *T. grossiseta*, it shows two highly specialized features not seen in *Lepidozia*: asexual reproduction by tubers and asexual reproduction by caducous or fragmenting leaf lobes. This suggests that evolutionary pathways within *Telaranea* diverge quite strikingly from those exhibited by *Lepidozia*.

1. **Telaranea tuberifera** Engel & Schust., sp. nov.

Plantae pallide olivaceae, mediocria, axe principali 1–1.4 mm lato. Folia (3-)4- lobata, 0.4–0.5 longitudinis divisa, lobis saepe caducis, ciliiformibus, partibus uniseriatis ex (4)5–6 cellulis constantibus; discus ± rectangularis, 5–6(7) cellulae longus; cuticula disci papillis densis et minutis instructa. Amphigastria 3–4 lobata; discus 2- vel ex parte 3-seriatus. Tubera reproductiva asexualia ad apices stolonium producta.

Holotype: New Zealand, South Is., Fiordland Natl. Park, Falls Creek, Upper Hollyford River Valley, along Milford Road, 3 November 1961, *Schuster 48775* (F).

Plants soft, flexuous, prostrate in dense compact mats, pale olive green in herbarium, whitish and highly nitid when dry, medium in size, the main axes 1–1.4 mm wide. Branches loosely to somewhat irregularly pinnate, but at times densely and regularly so, occasionally 2–3-pinnate; *Frullania*-type branches common, frequently elongating and remaining leafy, rarely stoloniform or becoming flagelliform; ventral intercalary branches also common, both leafy and stoloniform; stoloniform branches in turn frequently branched, the branches leafy or stoloniform. Stems with cortical cells thin-walled and in 12 rows, those on ventral side of stem somewhat smaller, the dorsal cortical cells much larger than medullary cells. Leaves on main axis rigid, fragile, the tips frequently ragged with varying parts missing, the leaves spreading nearly or at right angles to stem, rather densely imbricate; leaves basically (3-)4-lobed for 0.4–0.5 their length; lobes frequently caducous, ciliiform, consisting of a uniseriate portion of (4)5–6 cells long and a basal portion which is 2–4 cells wide at extreme base (the base sometimes consisting of only a pair of laterally adjoining cells). Discus ± symmetrically rectangular, often rather narrowly so; discus 5–6(7) cells long (from median sinus base to leaf base), 8–10 cells wide in distal portion, 8 cells wide at base, margins entire, the dorsal gently curved, the ventral straight. Cells of discus with walls thin, trigones absent, median discus cells 41–54 μm wide, 60–74 μm long; cuticle finely and densely striolate-papillose. Underleaves much smaller than leaves, strongly spreading, 3–4-lobed; lobes ciliiform, consisting solely of a uniseriate row of (2-)3(–4) elongated, thin-walled cells. Discus reduced, formed of 2 or in part 3 rows of cells high and 8(–9) cells

wide. Asexual reproduction by oval to ovoid tubers at the tips of stoloniform branches and probably by caducous leaf lobes.

Androecia and gynoecia not seen.

This new species is related to *T. centipes*, but differs from that species in possessing tubers, caducous leaf lobes, and ciliiform leaf lobes with their uniseriate portion being (4)5–6 cells long. *Telaranea centipes*, on the other hand, lacks tubers and has persistent leaf lobes which are subciliiform, with their uniseriate portion being 3–4 cells long.

This species, as the name we have chosen for the plant suggests, produces tubers. These are formed at the apices of prostrate, often ramified, microphyllous, ventral intercalary stolons that issue from older sectors of the plant (fig. 1: 10). The tubers are parenchymatous (fig. 1: 2,3,12) and bear scattered leaf rudiments on the surface (fig. 1: 2); the rudiments are unicellular or of 2 superposed cells, but in either case terminate in a slime papilla (fig. 1: 3). Such tubers seem not to "germinate" while remaining attached to a leafy stem. We have observed other tubers where the attachment to the "parent" plant was broken; these had "germinated," with the slender new shoots at first producing reduced, deeply bifid, few-celled leaves followed somewhat later by 3-lobed leaves (fig. 1: 2). It is notable that both 2- and 3-lobed leaves of germinating tubers often had at least a portion of the leaf lobe caducous, for this means that the caducous lobe feature is expressed ontogenetically very early, at least with regard to young axes from tubers.

The establishment of a tuber-bearing *Telaranea* is of considerable interest. In Hepaticae and Anthocerotales, ". . . the tuber is a special biological device evolved in taxa with extrinsically imposed short periods of growth. Tuber-bearing taxa are found principally in regions with a sharp alternation between wet and dry climates. . ." (Schuster, 1966, p. 531). Tubers are known, for example, in *Geothallus* (Sphaerocarpaceae); *Fossombronia*, *Petalophyllum*, and *Sewardiella* (all Codoniaceae); *Riccia* (Ricciaceae); and *Anthoceros* (Anthocerotaceae), and thus occur in four orders: Metzgeriales, Marchantiales, Sphaerocarpales, and Anthocerotales. The presence of tubers in *Telaranea* is remarkable then, for they were previously unknown for an entire order, Jungermanniales.

Yet there is more to the story of a tuberiferous *Telaranea*. *Telaranea tuberifera* is a plant known only from the rain forests of southern South Island, New Zealand (Fiordland Natl. Park), an area notable for its high rainfall. Two points are relevant in this connection: (1) the plant occurred along sides of a high waterfall; and (2) the tubers occur at the tips of prostrate rather than geotropic stolons, such that the tubers lie on the soil surface, rather than being buried within it. These points would seem to indicate that the tuber in *Telaranea* is not a perennation device, but rather is an asexual reproductive device, perhaps for the purpose of dispersal by water. Tuber cross sections, however, do not reveal aerenchyma, which might be expected in a structure specialized for water dispersal (fig. 1: 12).

Ecology-phytogeography: Known only from the type which is mixed with *Psiloclada clandestina* and was collected on steep slopes along the sides of a high waterfall.

2. **Telaranea grossiseta** (Steph.) Engel & Schust., comb. nov.

Lepidozia grossiseta Steph., Spec. Hep. 3: 584. 1909. *Neolepidozia grossiseta* (Steph.) Fulf. & J. Tayl., Brittonia 11: 85. 1959. Original material: Tasmania, *Moore (non vidi)*.

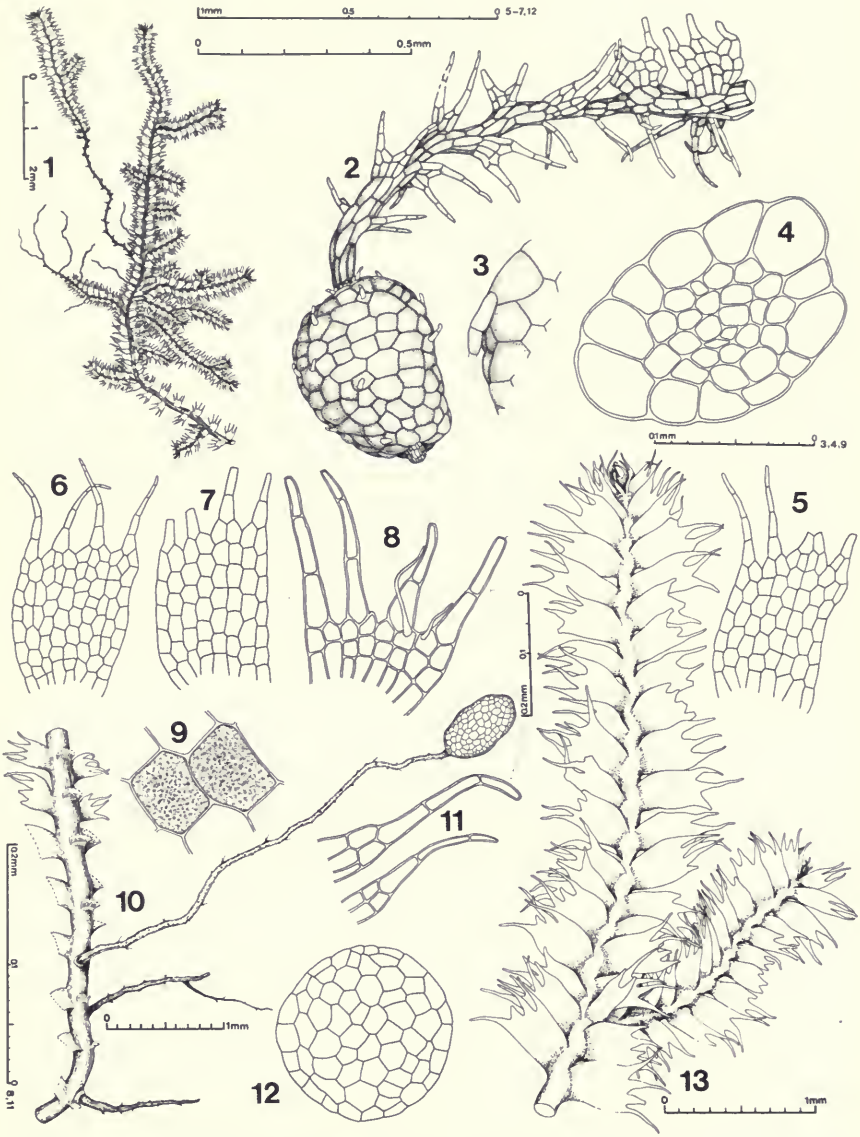

FIG. 1. *Telaranea tuberifera* Engel & Schust. 1. Plant, dorsal view. 2. Germinating tuber; note scattered leaf rudiments and previous point of attachment of tuber to stolon at opposing end of tuber. 3. Portion of tuber surface showing a leaf rudiment. 4. Stem, cross section. 5–7. Leaves. 8. Underleaf; note rhizoid position. 9. Median discus cells showing cuticular detail in part. 10. Old, basal portion of axis showing stoloniferous branches and a tuber. 11. First branch underleaves. 12. Tuber, cross section. 13. Portion of main axis; note ragged leaf apices. All from holotype.

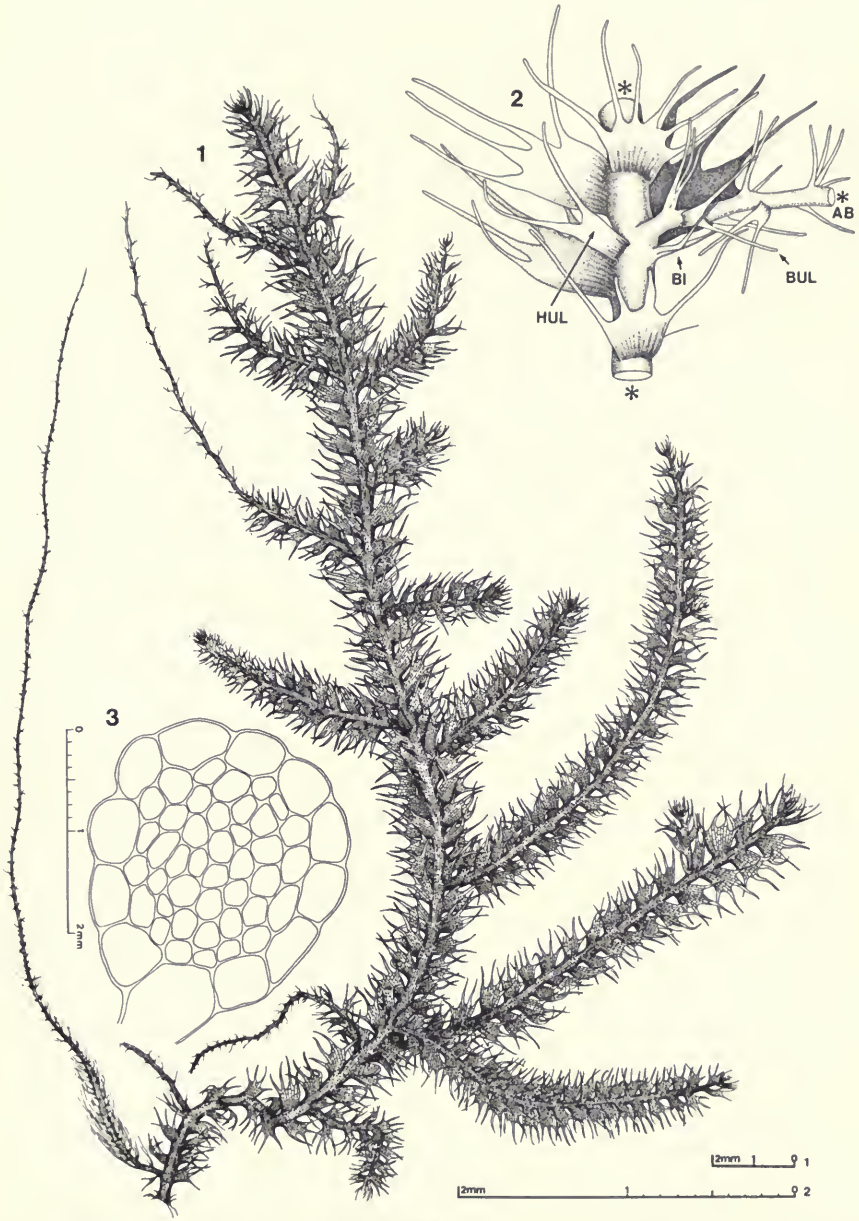

FIG. 2. *Telaranea grossiseta* (Steph.) Engel & Schust. **1.** Plant, dorsal view. **2.** Portion of main axis with *Acromastigum*-type branch (= AB), ventral view; note sexfid underleaf (rare) (HUL = half underleaf, BL = first branch leaf, BUL = branch underleaf. **3.** Stem, cross section. All from *Engel 14728*, Gordon River.

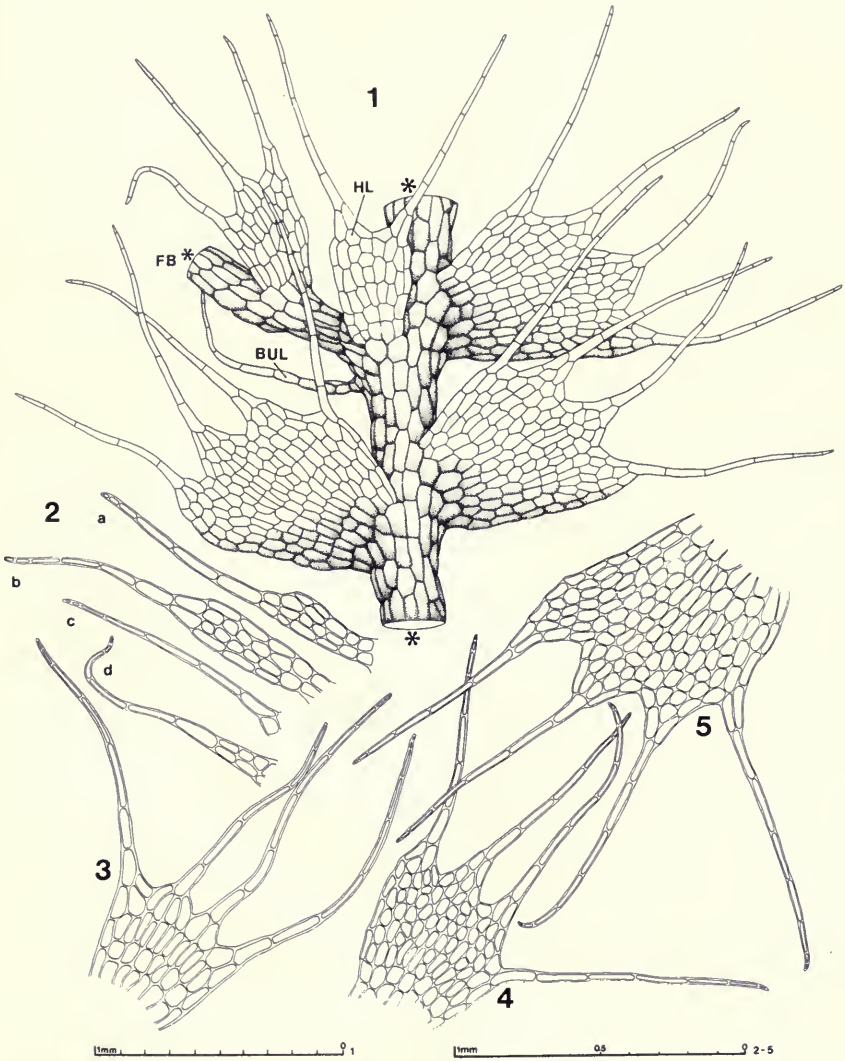

FIG. 3. *Telaranea grossiseta* (Steph.) Engel & Schust. **1.** Portion of main axis with *Frullania*-type branch (= FB), dorsal view (HL = half leaf, BUL = first branch underleaf). **2.** First branch underleaves. **3.** Underleaf. **4–5.** Leaves. All from *Engel 14728*, Gordon River.

This large species (main axes 1.6–2.2 mm wide) has 4-lobed leaves which are divided to 0.5–0.6 their length and have a well-developed discus. The leaf lobes are rigid and decidedly ciliiform, with the uniseriate portion composed of 6–7(–8), ± thick-walled cells (fig. 3: 1,4,5). The underleaves are 4(–6)-lobed, with the uniseriate portion composed of 6–9 cells. The underleaf discus is comparatively high for the genus, being 3–4 cells long (fig. 3: 3).

Telaranea grossiseta has predominantly *Frullania*- and ventral-intercalary branching, but rarely may produce *Acromastigum*-type branches, the latter being the first record of that branch type for *Telaranea*. Here the half underleaf is bifid (fig. 2: 2); the half leaf associated with *Frullania*-type branches is likewise bifid (fig. 3: 1). The first appendage of an *Acromastigum*-type branch is a bifid leaf (fig. 2: 2), whereas the first appendage of a *Frullania*-type branch is a ciliate to subulate underleaf (fig. 3: 1, 2).

The species is endemic to Tasmania.

Specimens seen: TASMANIA: Gordon River, vicinity of Sir John Falls, just upriver from Butler Island, ca. 50 m, *Engel 14728, 14733* (F); Cradle Mtn.-Lake St. Clair Natl. Park, W shore of Lake St. Clair ca. 1 mile N of Echo Hut, ca. 750 m, *Norris 28050* (F); Franklin River at Frenchman's Cap Trail crossing, ca. 400 m, *Norris 31194* (F); King River, 11.3 km by road from Regatta Point and 13.3 km by road from Strahan Harbour, stream that enters King River under wooden bridge, sea level, *Engel 14927* (F); road from Melba Flats to Confidence Saddle, 200–400 m, *Norris 31589, 31643* (F); Murchison River at Murchison Hwy., *Norris 33735* (F).

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